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THE FORM OF EVOLUTIONARY THEORY THAT MODERN GENETICAL RESEARCH SEEMS TO FAVOR

DR. CHAS. B. DAVENPORT

CARNEGIE STATION FOR EXPERIMENTAL EVOLUTION, COLD SPRING
HARBOR

Nature produces those things which being continuously moved by a
certain principle contained in themselves arrive at a certain end.

—Aristotle.

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I. GENERAL STATEMENT OF THEORY OF EVOLUTION

THE history of evolution, all will agree, has been from the less specialized to the more specialized. The prevailing view is that this greater specialization has been achieved by adding qualities one by one to the less specialized until there has become built up through the ages so complex structures as the higher types of organisms. Organic evolution, from this view, has proceeded along the same lines as the evolution of an old English manor

house through the accretions of successive generations; or is like some medieval cathedral to which each generation has added some sculptures, some stones to the steeple, some new stained-glass windows. Organisms, the theory runs, began simple,—they varied, why or how no matter; variation is given and is in all directions. Positive variations toward greater complexity were usually advantageous and individuals showing such elbowed out of existence their less-favored cousins and established a new and higher level from which evolution might proceed.

This view has certain resemblances to an old view of ontogeny. The embryo is simple. Food is added and food makes this part and that grow. Why only certain parts grow in the presence of food and not all—the differential nature of growth—that is *given*. It is the nature of the organism that all parts should not grow equally; but the essential thing is that food and water and heat are the things that add parts and make the embryo larger and more complex.

This view of development has, I think it will be admitted, now become generally abandoned. To-day we recognize rather that the egg or embryo is not so simple, but that, on the contrary, it has wrapped up in it all of the potentialities that are eventually realized; potentialities that will be realized, however, only if conditions of life (food, water, heat, etc.) are appropriate.

The alternative view of evolution, like the modern view of embryonic development, lays more stress on the internal factors of evolution. It postulates that the primitive organisms, like the eggs, are not so simple as they look but have a molecular constitution of great complexity; and, just as the egg has a mechanism by virtue of which (under favorable conditions) it develops, so the ancestral protoplasm had a mechanism by virtue of which (under favorable conditions) it *evolved*. We do not know much about the specific molecular machinery that determines the specific nature of differential growth, but

we have reason to think that it is located chiefly in the nucleus. Similarly we are ignorant of the specific nature of the machinery that determines phylogenetic variations, but we have reason to think that it is located in the germ plasm and that the karyokinetic phenomena, especially the movements of chromosomes at and around the time of fertilization, have a great deal to do with such phylogenetic change. But as the egg with its given internal mechanism of development under adequate external conditions will develop into the specific adult form, so the primitive germ plasm with its internal mechanism of evolution under adequate external conditions has developed into all those forms or kinds of germ plasm that are responsible for the great variety of present and past organisms. Just as the egg-nucleus contains probably fewer kinds of molecules, but each more complex, than a nerve cell, *e. g.*, of the adult, so the ancestral form of protoplasm probably contained fewer kind of molecules each more complex than the derived forms. The derived forms, conversely, have more kinds each of simpler constitution.

In this view (if we may let our imagination picture the consequences) the foundation of the organic world was laid when a tremendously complex, vital molecule capable of splitting up into a vast number of kinds of other vital molecules was evolved! The capacity for thus splitting off molecules determines the possibility of production of the organic species with their vast number of characteristics.

It is to be kept in mind, however, that the number of genes is probably less than the number of elementary species. For numerous elementary species differ by only one or two genes and in many cases the species differ only in new *combinations* of the same set of genes.

This theory of evolution is not new; it is that briefly expressed by Bateson in his Australian address; it is very clearly expressed by Hagedoorn in Roux's "Vor-träge" and has received the support of Lotsy (1913). It

is, however, essentially Nägeli's theory of evolution from within by virtue of a perfecting or progressive tendency, in support of which Nägeli himself draws the parallel between embryology and evolution. It has certain points of resemblance to Eimer's orthogenesis, but differs from it tremendously in that Eimer thought evolution was directed by the external world and that there were summed in the germ plasm the impressions of that world received in successive generations. Huxley was inclined to accept the theory of internal factors in evolution. He says:

I apprehend that the foundation of the theory of natural selection is the fact that living bodies tend incessantly to vary. This variation is neither indefinite, nor fortuitous, nor does it take place in all directions, in the strict sense of these words. . . . A whale does not tend to vary in the direction of producing feathers, nor a bird in the direction of developing whalebone.

Mivart and many others have long contended that evolution is due to *internal* factors. Their views are in accord with Aristotle's.

Finally, I may close this section by quoting a simile from Bergson, as translated by Mitchell.

The evolution movement would be a simple one, and we should soon have been able to determine its direction, if life had described a single course, like that of a solid ball shot from a cannon. But it proceeds rather like a shell, which suddenly bursts into fragments, which fragments, being themselves shells, burst in their turn into fragments destined to burst again, and so on for a time incommensurably long. We perceive only what is nearest to us, namely, the scattered movements of the pulverized explosions. From them we have to go back, stage by stage, to the original movement.

When a shell bursts the particular way it breaks is explained both by the explosive force of the powder it contains and by the presistance of the metal. So of the way life breaks into individuals and species. It depends, we think, on two series of causes: the resistance life meets from inert matter, and the explosive force—due to an unstable balance of tendencies—which life bears within itself.

II. SUPPORT FOR THE THEORY FROM COLLATERAL FIELDS

The view that the course of evolution (like the development of the individual) is chiefly determined by internal

changes receives support from various collateral fields of investigation.

1. First, from *embryology*, by analogy. The development of the embryo is directed from within. The process of development is one of specialization; a great number of tissues is produced but these tissues have lost the capacity, which the embryo has, of producing all kinds of tissues. Development is essentially an irreversible process just as evolution is, and for the same reason—that a fragment can not produce the whole. The adult individual is more complex than the fertilized egg, yet the egg has greater potentialities than any tissue-cell has. Regeneration depends on the presence of embryonic, *i. e.*, non-tissue, cells lying latent amidst the tissue cells. The greater complexity of the adult as a whole over the egg does not hold for a given tissue cell—that is *less complex* than the egg. The complexity of the adult is due to the fact that there are in the body many kinds of tissue cells, each simple, while the egg is just one kind of cell—but very complex in constitution. Similarly, we may infer that while the vast number of *kinds* of germ plasms in the higher organisms, differentiated in respect to their chromomeres, contrasts with the condition in the protista, it is probable that each chromomere of the protista is composed of much more complex organic molecules or molecule complexes.

2. Another mass of evidence for this theory is supplied by *paleontology*. By this science are offered extensive series showing: (*a*) the usual beginning of a new character as a simple, often inconspicuous trait, (*b*) the increase of variety in the course of evolution of a phylum ending in great outburst of extreme and bizarre forms immediately preceding the extinction of a phylogenetic line; (*c*) the irreversibility of the process of evolution; and (*d*) parallelism in evolution of allied lines.

(*a*) *The Simple Beginning of a Trait*.—The early history of a number of spinose groups of species shows (Beecher, 1898) that each group began its history in

small, smooth or unornamented species. The septæ of ammonites begin simple and later evolve their extraordinary foldings. The horns of titanotheres "have excessively rudimentary beginnings phylogenetically, which can hardly be detected on the surface of the skull" (Osborn, 1912, p. 253). Also, these "rudiments arise independently on the same part of the skull in different phyla at different periods of geological time."

(b) *The History of Progressing Phylogenetic Development*.—While paleontologists have no knowledge of germinal conditions they can study the course of evolution of a particular character through a lineage comprising thousands of generations. Paleontologists are agreed that characters tend to become more and more complex. So Beecher (1898, p. 354) writes:

The smooth, rounded embryo or larval form [terms used in the phylogenetic sense] progressively acquires more and more pronounced and highly differential characters through youth and maturity. In (paleontological) old age, it blossoms out with a galaxy of spines, and with further decadence produces extravagant vagaries of spines. So in the titanotheres the horn rudiments evolve continuously, and they gradually change in form, . . . they finally become the dominant characters of the skulls, showing marked variations of form in the two sexes.

The saber-toothed and other tigers gained canines that they could not use. The mollusc, *Hippurites*, gains a shell a foot thick. In the Labyrinthodonts the infolding of the teeth has been carried to an extraordinary degree, etc. These are illustrations merely of what is said to be a general rule. F. B. Loomis¹ writes of it under the head "Momentum in Evolution."

(c) *The Irreversibility of the Process of Evolution* has been often remarked upon. It leads to exaggerated developments in one direction; lateral and backward variations are relatively uncommon.

Thus, the horse has shown divergent lines of evolution but none returning to the four-toed ancestral type. The ammonites went from simpler forms of septum to more and more complex without reversal, except at the very end of their phylum. D. Rosa says:

¹ AMER. NAT., 39 (1905).

An organ which in the course of its phylogenesis once disappears has disappeared for ever. . . . Not an exception is known to the rule.

Even an organ once rudimentary, like flying in some ground birds, never returns to full activity. A striking example of dropping out is that of cilia in Arthropods; which, ubiquitous in other groups of animals, are in this group gone throughout; they fail to develop even in spermatozoa. Toward the end of the process of evolution, a character tends to break up into a great number of new characters. These usually affect a certain organ, like the suture of the ammonites, and precede extinction of the phylum. We may say that the number of genes has become, through fractionation, so great that the resulting complexity or the resulting extremes of development of a trait are prejudicial to the development of the organism.

(d) *Parallelism of Evolution in Allied Lines*.—This parallelism was recognized by Darwin who writes:

The principle formerly alluded to under the term of *analogical variation* has probably in these cases often come into play; that is, the members of the same class, although only distantly allied, have inherited so much in common in their constitution, that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs, strikingly like each other, independently of their direct inheritance from a common progenitor.

Of such parallel variations Osborn (1915, p. 216) speaks as follows:

Similar rectigradations may arise in all the descendants of similar ancestors at different periods of time; they always give rise to parallelism or convergence between the members of related phyla.

Illustrations of such are afforded in many paleontological monographs.

3. Another line of evidence for the theory of the primacy of internal factors of evolution is found in *experimental breeding*. This evidence appears in the facts (a) that many mutations begin small and can be rapidly evolved into highly developed characters, (b) that similar variations appear in related organisms, (c) that

mutation is limited to certain lines and (d) that experimental evolution seems *chiefly* due to dropping out of genes.

(a) That *characters often arise as rudiments* and only in the course of generations realize their full potentiality is a well-known experience of breeders. Thus De Vries² states that the double *Anemone coronaria* was produced by the owner of a nursery who, observing in his beds a flower with a single broadened stamen, saved its seeds separately and in the succeeding generations procured beautifully filled flowers. By appropriate matings Castle succeeded in 5 generations in getting much better expressed polydactylism in guinea pigs than he had at the outset. Dr. F. E. Lutz (1911) found a slight abnormality of venation in the fruit fly, *Drosophila ampelophila*. By in-breeding abnormally veined flies and selecting as breeders the extremely abnormal flies he eventually secured in the later generations some highly abnormal individuals. From a hen that showed only a slight extension of the web between certain toes I succeeded in breeding a race of profoundly syndactyl descendants.

(b) That *mutations ("saltations") run in parallel lines* in related species is well brought out in a table given by Osborn (1912, p. 191), which I reproduce here with certain modifications.

That each germ plasm can vary only within certain limits and that related germ plasms show only a limited number of variations and the same in the different species indicate that variations of the specific rank are not determined by anything outside the organism, but by the very nature of the organism. Thus, the rabbit shows in its coat color the agouti coloration, and so does the guinea pig. From this in the guinea pig have arisen yellow, chocolate, black, albino and other colors; and a similar series has been obtained for rabbits. The guinea pig has produced an angora coat and so has the rabbit,

² "Species and Varieties," p. 491.

COMPARATIVE TABLE OF SALTATIONS

	1	2	3	4	5	6	7	8	9	10	11
	Man	Horses	Cattle	Sheep	Deer	Pigs	Dogs	Cats	Rabbits	Guinea Pigs	Mice
1. Proopic brachycephaly, abbreviation of face.....	..	..	×	..	..	..	×	..	..	..	..
2. Sudden development of horns on hornless races.....	..	×	..	..	..	..	..	..	×	..	..
3. Absence of horns on horned races..	..	..	×	×	..	..	..	..	..	..	..
4. Jaw appendages.....	×	..	..	×	×	..	..	..	..	..	..
5. Taillessness, absence of caudals...	×	×	..	×	..	..	..	×	..	×	..
6. Short-leggedness, or limb abbreviation.....	×	..	×	×	..	..	×	..	..	..	..
7. Consolidation of paired hoofs, syndactylism.....	×	..	×	..	..	×	..	..	..	..	..
8. Polydactylism.....	×	×	×	×	×	×	×	×	..	×	..
9. Epidermal thickenings.....	×	..	×	..	..	..	..	..	..	..	×
10. Mottled skin markings.....	×	×	×	..	..	×	..	..	..	..	..
11. Excessive hairiness, or length of hair.....	×	×	×	×	..	..	×	×	×	×	..
12. Hairlessness, entire absence of hair.....	×	×	×	..	..	..	×	..	..	..	×
13. Excessively fine or silky hair.....	×	..	×	×	..	..	..	×	×	..	×
14. Reversed hairs.....	×	..	×	..	..	..	..	..	×	×	..
15. Curled-hair.....	×	×	×	×	..	..	×	..	..	..	..

the cat, the dog, the goat, the sheep (Lincoln) and others. So in different species of *Drosophila*, I am informed by Dr. C. W. Metz, the same mutations occur—of course, without any relation to environment.

In a strain that has produced a mutation once we are apt to find the same mutation a second time. Thus De Vries states that the peloric toadflax does not set seed in nature, yet it occurs repeatedly in a given locality and even in distant localities. We conclude there is something in the structure of the germ plasm of the toadflax that permits a wholly useless, and indeed not naturally perpetuated, mutation to occur easily. Similarly, doubling of the floral parts occurs again and again in wholly unrelated species; often combined with complete sterility. Again, poultry sometimes show a great extension of the web between the toes. This occurs chiefly between digits III and IV, exactly where the syndactyl web occurs in man and where it occurs in wading birds that have only a single web between the toes—of which 8 genera might

be named. So far as I know, a marked extension of the web between digits I and II has never been observed; between II and III it is relatively rare; again, between IV and V it has, so far as I know, not been noted in mammals.

(c) *Variation is Not Indefinite and Multifarious.*—The case of syndactylism in poultry well illustrates the general principle of the *limitation* of mutation to particular narrow lines; and this is commonly the case. Thus, Dr. J. A. Harris has examined himself and with the assistance of others over 1,000,000 bean seedlings, and while extraordinary variations have been found, yet in the later hundreds of thousands no new ones have appeared; nevertheless, the possibilities in leaf form, variegation, etc., if we may judge from books on plant teratology, are by no means exhausted. And when we contemplate the variety of form assumed by first leaves in different species, is not the constancy in the form in beans striking evidence of the narrowness of variation and its restriction to certain lines?

(d) *Evolution by Loss of Genes.*—Finally, it has long been recognized that an extraordinarily large proportion of the mutations we meet with are recessive to the wild type. Castle has noted this of rabbits and guinea pigs³ and Morgan has noted it in the case of *Drosophila*. In my work with poultry I was not impressed with it, as taillessness, polydactylism, syndactylism, white color of the Leghorn, rose comb, etc., are dominant mutations. Still, other genetics work (Baur, Shull and many others) is strengthening the conclusion that current evolutionary changes under observation are chiefly due to the dropping out of genes, and this supports the theory that evolution is proceeding largely by the loss of genes. However, the fact of dominant mutations can not be derived. Take, for instance, foot abnormality. Here a disturbing factor has appeared in the organism that was not there before. There is no *a priori* reason for doubting that the break-

³ "Heredity," p. 86.

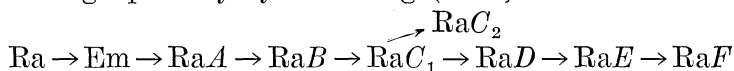
ing up of one of the genes that makes for the normal foot might have a residuum that positively interferes with the operation of other foot-forming factors.

The genetical studies also accord with other evidence as to the general irreversibility of evolution. We see that when a population contains only a recessive trait it is impossible by breeding inside that population to get back the dominant allelomorph. From a pure blue-eyed population we do not get back the primitive brown-eyed condition.

It might be thought that if evolution proceeds chiefly by loss of factors it would tend to simplification rather than increase of the number of factors. It seems probable, however, that the loss is not merely of a whole gene, but of some part of it; a fractionation, as it were, by which the gene becomes altered or split up into two or more. For example, it is probable that in man the loss of a gene (or a part of one) releases special nervous states, as, for instance, that in which musical combinations run through the brain, or numerical relations are rapidly worked through, etc. Thus the *general* result of experimental work in genetics gives support to the view of evolution by loss of genes and by their fractionation.

4. *Evidence from Evolutionary Changes in the Inorganic World. Radiation Studies.*—The view that evolution is primarily by internal changes receives unexpected support from the recent discoveries concerning the evolution of the elements. It is now well known that the element, uranium, under certain conditions of temperature, etc., undergoes a spontaneous change into ionium, ionium into radium, radium into polonium, an essentially lead-like substance. Similarly, thorium passes through mesothorium and radiothorium. Indeed, in a particular series, side branches may be given off; thus polonium is not derived directly from radium, or from radium *C*, but from one form of radium *C* called radium *C*₁. Indeed, “radiums” of different sorts, called radium *A*, radium *B*, radium *C*, are recognized and the atoms of these differ

from one another by, probably, one electron lost from each successive stage of the series. The series is thus shown graphically by Sieveking (1913):



III. CERTAIN CONSEQUENCES OF THE THEORY

1. The acceptance of this theory requires a special *explanation to account for adaptation*. Eimer's theory of orthogenesis posited the direct action of environment on the germ plasm, a view which wider knowledge of facts does not support. It follows naturally from the hypothesis that new traits bear, at first, no relation to environment any more than the polonium that is derived from the uranium does. Darwin recognized that variations were not necessarily adaptive in their origin; also that it was not necessary that they should be adaptive in order to survive. Darwin says:⁴

We clearly see that the nature of the conditions is of subordinate importance in comparison with the nature of the organism in determining each particular form of variation.

How then is adaptation brought about? Strictly, we may say adaptation is not the thing that is brought about, but rather absence of non-adaptiveness. Such adjustment as we find is, doubtless, only such a residuum of variants as has not proved incompatible with conditions of existence. Two kinds of variations may survive: (a) Those not incompatible with the conditions of the present environment and (b) those which, while incompatible with present environment, are not incompatible with some other environment into which the species may migrate.

2. *Relation to the Rôle of Selection in Evolution.*—There is going on to-day a great discussion as to the importance of selection in evolution. How does the matter look from the standpoint of this theory.

First, all are agreed that nothing has importance for

⁴ "Origin of Species," p. 9.

evolution of the race except what modifies the germ cells, because they are all that goes from one generation to the next. However, we learn little or nothing about the potential traits of the germ cells by looking at these cells. Our knowledge of their hereditary composition depends upon the traits shown by the individuals that develop out of them. We may infer the genotype by observing the phenotype. But the phenotypical condition of a person is a more or less imperfect index to the genotypical condition of that person. The soma is an imperfect index to the germ plasm. The difference between the two schools, one asserting, the other denying the value of "selection," is based primarily upon the reliance placed on the sufficiency of this index. Castle says, in effect, the somatic condition of my rats in respect to the coat-pattern is so good an index of their germinal condition that whenever I select rats for a quality of the pattern I am selecting them very closely for the corresponding quality of their germ plasm. Pearl says, in effect, in poultry the egg-laying capacity of the hen is hereditary; yet it is so poor an index of her germinal idiosyncrasies in this respect that an individual with the somatic characters of high laying is no more apt to have the genes for high laying than an individual with the somatic character of low laying. Pearl says to make progress I must select for breeders those which have proved their germinal quality by belonging to a race of high layers. If the various sisters and daughters of the hen are high layers, that is more important than the egg-laying performance of the one individual, merely.

It seems to me that the whole question is a pragmatistical one. If the somatic condition of a trait is a good index of germinal conditions, in any case progress can be made by selecting the soma in that case; if the soma is an inadequate index, then little or no progress will be made by selecting the soma. We know this by breeding experience. If we select parents because of absence of pigment in skin or eye, we select also a germ plasm devoid of the

capacity for forming such pigment. If we select parents because they have medium-brown hair we get offspring with blond or golden or red hair even, and it would take a long time to get a pure brown-haired race by this method of selecting. If the trait that we are trying to improve is very sensitive to environment, then the somatic conditions will be a very bad index of the germinal; but if not sensitive, the somatic may be a good index of the germinal. Thus, since in the fruit fly the number of bristles varies closely with food conditions, selection of breeders merely on the somatic state will not lead to much, if any, genetic progress.

The question of the potency of selection in nature comes back to the matter of value of the soma as an index of the germ plasm. If blue eye color affords insufficient protection from tropical conditions elimination of the blue-eyed individual kills off blue-eyed plasm and with each death the race is rapidly purified. But there is a limit to the process because brown eyes are preserved equally whether the germ plasm does or does not carry the blue-eyed condition. As there are twice as many simplex as duplex brown eyes, the complete elimination of the blues will not be brought about quickly.

When, therefore, we hear a breeder say: "I made this character by *selection*" what he really means is: Somatic variations in the desired direction were afforded; there was a large correlation between somatic and germinal conditions, so that I was able, merely by choosing as breeders individuals showing the desired trait somatically, to get a race with the determiners of the character pure, or practically pure, in the germ plasm.

One other difference of opinion there seems to be between selectionists and the others. Castle evidently doubts if factors for characters are always discrete and do not change. He is inclined to hold that there may be genes which vary *pari passu* with a variation of a "unit character" and in somewhat the same degree. This view seems to be quite in accord with an expectation that

is based on experience, that traits shall be found the germinal bases of which are undergoing current evolutionary changes through loss of genes or through fractionation. And it is in accord with expectation that mutations shall reveal themselves just at the extreme of a series as Castle's plus mutation revealed itself. Others are inclined to think that the varied color pattern of Castle's rats is really determined by several factors (restrictors or extensors of the gene for "hoodedness") which were all in his race of rats at the beginning of his experiment. Upon one point all geneticists are, however, agreed—that we must interpret all of our results in terms of genes alone.

One other bearing of the orthogenetic theory deserves to be pointed out. If the germ plasm is capable of undergoing a spontaneous mutation which is the main source of evolutionary change, this fact would seem, at first blush, to indicate the futility of trying to control genetic change experimentally, except by the selection of germ plasms. Naturally, under these circumstances our effort would be limited to what nature affords. However, we do not yet know enough to put these limits on "experimental evolution." There is some evidence, although not as critical as might be wished, that the germ plasm is not beyond the reach of modifying agents. At least we must continue experimental efforts in that direction.

IV. SUMMARY

A theory of evolution that assumes internal changes chiefly independent of external conditions, *i. e.*, spontaneously arising, and which proceeds chiefly by a splitting up of and loss of genes from a primitively complex molecular condition of the germ plasm seems best to meet the present state of our knowledge.

Such a theory receives support from various fields.

1. From ontogeny, where the differentiated end stage is derived from a relatively undifferentiated, but probably molecularly complex egg.

2. From paleontology, where the history of the phylum seems governed by internal laws.

3. From experimental breeding where progress is afforded only as internal changes permit.

4. From analogy, with evolution in the inorganic world, so far as may be inferred from the studies on the "rare earths."

Such a theory makes clear that success in "selection" depends on rate and amplitude of internal change and ability to judge of germinal from somatic conditions.

It renders less hopeful (but not hopeless) the prospect of being able to control completely by experimental methods evolutionary change.

CARNEGIE INSTITUTION OF WASHINGTON,
STATION FOR EXPERIMENTAL EVOLUTION,
COLD SPRING HARBOR, LONG ISLAND, N. Y.

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